TABLE 1. Incidence of distress calls in species handled separately by two workers.

Species	Handler A N	Handler A % callers	Handler B N	Handler B % callers
White-ruffed Manakin *Corapipo altera*	6	0	23	0
Bicolored Antbird *Gymnopithys leucaspis*	6	100	8	50
White-breasted Wood-Wren *Henicorhina leucosticta*	6	100	6	33
Silver-throated Tanager *Tangara icterocephala*	11	74	6	0

Birds were captured and subsequently released. They were considered callers if they gave a distress call as the handler approached the net, during removal from the net or during handling afterwards.

Four species yielded samples large enough for statistical comparisons among handlers (Table 1). In these species the percentage of birds that called was highly significantly affected by who handled each bird (the appropriate contrast in a 3-way G-test of independence [Sokal and Rohlf 1969], $G = 23.504$, $P < .005$). Presumably the differences in caller percentages occurred because the workers handled birds differently. We do not know what kinds of handling differences occurred. They may have included length of time in the net, duration of handling, position of birds during handling or gentleness of handling.

The handler effect emerges as an influence on the incidence of distress calls by netted birds. Of 26 species with samples of 4 or more handled by Meyer, Patti and the authors in Costa Rica, 9 (35%) called with a frequency of 26–75% and should be classified as "intermediate." In the study by Rohwer et al. (1976), 9 of 29 species (31%) would be similarly classified. Clearly this category may be a result of the differences between handlers discussed herein.

Recognition of the handler effect demands that workers standardize their methods before comparing or combining results. The incidence of calling may be as much a result of the method of handling as it is a characteristic of the species. Future examination of distress-call behavior should involve observations of captures by a variety of natural predators, each of which may handle birds differently and elicit a different response. The reasons why some individuals of some species call and others do not are still obscure.

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THE RELATIONSHIP BETWEEN HABITAT AND SONG IN THE WHITE-THROATED SPARROW

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Habitat acoustics have played an important role in the evolution of long-distance avian vocalizations (Ficken and Ficken 1963, Morton 1970, 1975, Chappuis 1971, Jilka and Leisler 1974, Marten and Marler 1977, Marten et al. 1977). In tropical forested environments songs tend to be lower pitched, span a narrower range of frequencies, and to be more tonal than songs given by birds of open fields (Morton 1970, 1975, Chappuis 1971). Morton was able to predict these results from sound propagation tests he made in forest and grassland in Panama.

Recently, Marten and Marler (1977) tested sound attenuation in various temperate zone habitats. They found that the height from which a vocalization is given, the frequency (Hz) of the signal, and the habitat affect sound transmission. Upon close examination of their results, one can predict that birds living in a forested temperate zone environment are more likely to sing lower frequency songs than conspecifics residing in a field.

In Danbury and Wilmot counties, New Hampshire, White-throated Sparrows (*Zonotrichia albicollis*) breed in fairly homogeneous habitats which are in various stages of forest regeneration. In this paper I investigate intraspecific differences in songs associated with these habitats, and test the prediction that birds living in forests sing lower frequency songs than those living in fields.

MATERIALS AND METHODS

Male White-throated Sparrows sing songs of only one, or occasionally two, patterns. From 1973 to 1976, using a Uher 4000 Report-L tape recorder and a Dan Gibson (model P-200) parabolic microphone, I recorded 146 song patterns from 141 White-throated Sparrows (five birds sang two patterns). I base my results on this sample, disregarding the problem of more than one pattern

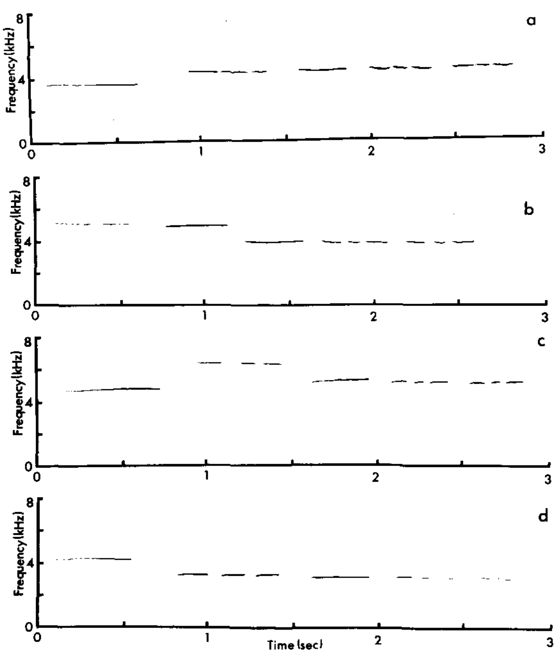

FIGURE. 1. The major song categories: (a) low-high, (b) high-high-low, (c) low-high-medium, and (d) high-low.

per bird. I recorded ten songs for each bird on at least two occasions during the breeding season. I made all recordings between dawn and one and one-half hours after sunrise.

I analyzed one randomly-selected recording, for each of the 146 song patterns, with a Kay 6061-B Sonograph, using the FL-1, linear scale, and narrow band filter settings. From the spectrograms I measured the frequencies of the first, second, and third notes. Lemon and Harris (1974) reported that the estimated predominant frequencies of the notes in the White-throated Sparrow song have coefficients of variation of less than 2%. I found coefficients of variation of less than 2.5% for the mean frequencies of the first three notes (23 birds, 10 songs per bird). Hence, the frequencies of the first, second, and third notes are highly stereotyped within the individual.

I categorized birds as residing in either field or forest. During the four-year study, eight forest and four field habitats were investigated. All 12 areas were within 10 km of each other. The predominant vegetation in the field was low spreading evergreen shrubbery (*Juniperus communis*) about one meter tall and often several meters in diameter. Hemlock (*Tsuga canadensis*), spruce (*Picea* sp.), birch (*Betula papyrifera*), and pine (*Pinus* sp.) were scattered throughout the fields. Forest was characterized by mixed coniferous and deciduous woods, at least five years more advanced in succession than the fields. Random 10-m transects were run through both the field and forest habitats. Average stem diameters and heights of the plants in the transects (rounded to the nearest whole number) are reported in Table 1. Only plants (1) greater than 50 cm in height, and (2) breaking the vertical plane of the transect were included in the results. The stem diameter (chi-square = 29.70, df = 2, $P < 0.001$) and height (chi-square = 47.17, df = 3, $P < 0.001$) of plants in the forest were significantly greater than the diameter and height of plants in the field.

RESULTS

Looking at the relative frequency (Hz) of the notes within a song, I found four major categories in which I could fit all 146 song patterns:

(I) One low note followed by a series of higher notes (Fig. 1a). Songs which included a very short note after the second high note (described by Borror and Gunn 1965) were included in this category.

(II) Two high notes followed by a series of lower notes (Fig. 1b).

(III) One low note, followed by a high note, followed by intermediate notes (Fig. 1c).

(IV) One high note followed by a series of lower notes (Fig. 1d).

Since the first note of the song of the White-throated Sparrow has been shown to convey information about individual and species recognition (Falls 1969), I compared the absolute frequency (Hz) of the first note among the song categories. After pooling the field and forest data a one-way analysis of variance on the frequency (Hz) of the first note indicated a difference between categories (F = 94.25, df = 3, 142, $P < 0.001$) and all four song categories were different from one another (Student-Newman-Keuls test, $P < 0.05$). The second note also differed between categories (F = 57.04, df = 3, 142, $P < 0.001$) and again all four song categories differed from one another (Student-Newman-Keuls test, $P < 0.05$). The two highest-pitched song categories (based on the first and second notes) low-high-medium, and high-high-low, were more likely to be associated with the field than the forest (chi-square = 10.27, df = 3, $P < 0.05$, from total number of songs in each category and habitat, Table 2).

Low-high songs from the field were significantly higher in frequency (Hz) than low-high songs from the forest (Table 2, first note, t = 3.00, df = 106, $P < 0.01$; second note, t = 2.70, df = 106, $P < 0.01$). The high-high-low, and high-low songs were not significantly different between the field and forest ($P > 0.05$). I did not compare low-high-medium songs from the field and forest because there was only one low-high-medium song from the forest.

DISCUSSION

For birds singing more than two meters off the ground, the frequency of a signal is related to excess attenuation (i.e. the higher the frequency the greater the excess attenuation). Within the frequency range of the White-throated Sparrow (2,150–6,500 Hz, Borror and Gunn 1965), for a bird singing from five to ten meters off the ground (typical of this species), this ef-

TABLE 1. Vegetation analysis based on transects run through field and forest habitats.

	No. of transects	Average number of plants with a diameter			height			
		< 1 cm	1–10 cm	> 10 cm	0.5–1 m	1–5 m	5–10 m	> 10 m
Field	4	64	4	1	65	3	1	0
Forest	8	12	10	6	8	10	4	6

TABLE 2. Measurements of four major categories of song patterns in forest and field. N equals the total number of song patterns I found in a given category and environment.

Category		Average frequency (Hz ± 1 S.E.)			N
		1st Note	2nd Note	3rd Note	
I. low-high	Field	3,370 ± 40	4,110 ± 60		77
	Forest	3,100 ± 90	3,810 ± 90		31
II. high-high-low	Field	4,910 ± 120	4,840 ± 130	3,850 ± 100	15
	Forest	4,920 ± 120	4,860 ± 100	3,960 ± 200	2
III. low-high-medium	Field	4,430 ± 60	5,750 ± 110	4,970 ± 40	14
	Forest	4,000	4,760	4,560	1
IV. high-low	Field	4,100 ± 260	3,270 ± 50		2
	Forest	3,950 ± 360	3,680 ± 290		4

fect is stronger in a forest than in a field (Marten and Marler 1977). Therefore, forest-breeding White-throated Sparrows would derive a greater selective advantage by singing a low frequency song than would field-breeding birds.

Even though White-throated Sparrows do not possess a dialect as such (Lemon and Harris 1974), it appears that song categories are distributed as a mosaic, separated by habitat. Higher frequency songs are associated with a field environment and lower frequency songs with a more forested environment. The closely related Rufous-collared Sparrow (*Z. capensis*) apparently also shows some separation of theme frequency by habitat (King 1972). Birds singing particular songs might be associated with habitats where they have "local adaptations" (Nottebohm 1972) for more efficient use of resources, predator avoidance, or both. Females may then obtain a selective advantage by recognizing differences in songs and choosing mates who were raised in the same habitat that they were.

SUMMARY

I recorded 146 different song patterns from 141 White-throated Sparrows. All the patterns could be fitted into four major categories according to the relative frequency of the notes within a song. The higher frequency (Hz) categories (based on the first and second notes) were more likely to be associated with the field than the forest.

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